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DO BROWN-HEADED COWBIRDS LAY THEIR EGGS AT RANDOM IN THE NESTS OF RED-WINGED BLACKBIRDS?

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Abstract.—We tested the hypothesis that female Brown-headed Cowbirds (*Molothrus ater*) deposit their eggs randomly in nests of Red-winged Blackbirds (*Agelaius phoeniceus*) by analyzing the weekly distributions of numbers of eggs in the nests of potential hosts with Poisson distributions including and excluding the zero-class. The hypothesis that females laid randomly could not be rejected in any weekly period when either all nests were included or when only parasitized nests were used. However, when all data were pooled, a random hypothesis using all nests could be rejected because there were more nests without cowbird eggs than expected. Among parasitized nests, a random hypothesis could also be rejected because there were more nests with a single cowbird egg or with 3–5 cowbird eggs than expected. Our results illustrate the importance of examining distributions with respect to the opportunities actually available to laying cowbirds. Pooling data from entire seasons may give misleading results. *Received 10 Aug. 1988, accepted 25 March 1989.*

The Brown-headed Cowbird (*Molothrus ater*) has been reported to parasitize more than 200 different North American bird species (Friedmann 1963, Friedmann et al. 1977, Friedmann and Kiff 1985). Some information is available on how cowbirds locate nests (Robertson and Norman 1977, Payne 1977), but little is known about how laying females choose from among available nests. If females do not discriminate among nests, but simply lay randomly in the nests they find, the proportions of nests with 0, 1, 2, 3, 4, . . . i cowbird eggs should approximate a Poisson distribution (Preston 1948, Mayfield 1965). Some authors have found non-random distributions of parasitized nests (Elliott 1977, Linz and Bolin 1982, Lowther 1984, Preston 1948), whereas others have found support for a random model (Mayfield 1965). From these analyses authors have drawn conclusions about choices of nests by female cowbirds.

It is difficult, however, to infer patterns of laying behavior from such statistics because deviations from random egg laying can be caused by many factors. Some, such as: (1) partial non-overlap between laying dates of parasites and hosts, (2) combining data from different acceptor species that are heavily or lightly parasitized, (3) inclusion of rejector species in the sample (Mayfield 1965, Rothstein 1975), and (4) desertion of parasitized nests, making them less likely than active nests to be found by

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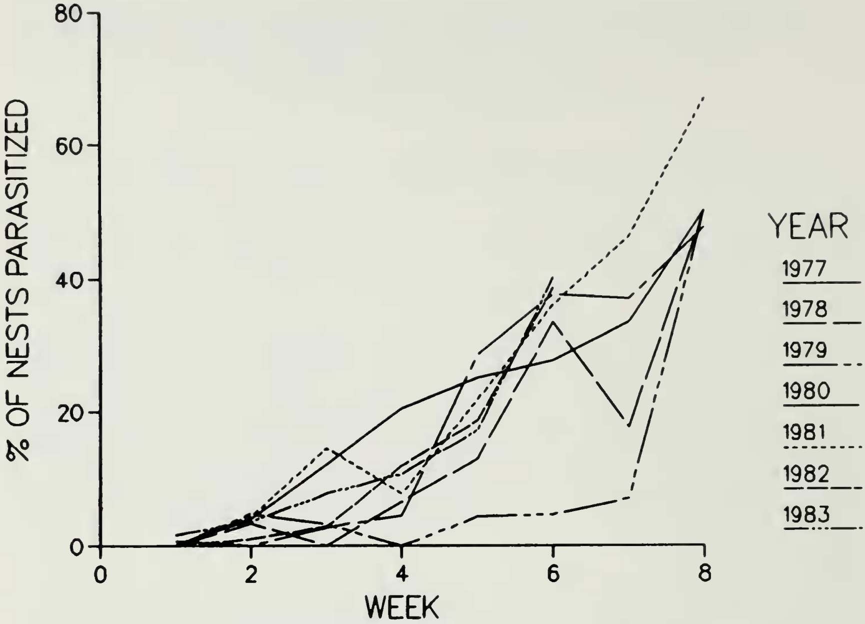

FIG. 1. Percent of Red-winged Blackbird nests parasitized by Brown-headed Cowbirds, by week, for the years 1977 through 1983 (week 1 = fourth week of April, week 8 = third week of June).

human observers, result in artifacts that do not reveal anything about choices by laying female parasites. Others, such as: (5) unequal ease in finding nests by parasites, (6) effective nest defenses by hosts (Robertson and Norman 1976), (7) an excess of nests to parasitize, and (8) an avoidance of already parasitized nests by laying females reveal aspects of choices by female parasites and their interactions with potential hosts. In this paper we show how the ways in which data are pooled for analysis may affect interpretation of field data on patterns of brood parasitism.

It is important to be able to identify how parasitic females choose the nests in which they lay, because the success of parasites may depend, in part, upon the types of discriminations they perform and because the evolution of responses by hosts may be related to the ways in which parasites choose hosts. To examine these choices more closely, we studied cowbird parasitism of the Red-winged Blackbird (*Agelaius phoeniceus*) in an area where redwings were by far the most abundant host for cowbirds. By concentrating on a single, abundant host species, we were able to assess laying behavior of cowbirds in relation to the availability of host nests at the time the females were making their choices. Thus we were

TABLE 1

SEASONAL PATTERN OF INITIATION OF NESTS OF RED-WINGED BLACKBIRDS AND LAYING OF EGGS BY FEMALE BROWN-HEADED COWBIRDS

Week	New nests	Parasitized nests	Cowbird eggs	Cowbird eggs/new nest	Eggs/parasitized nest	% of nests parasitized
IV Apr	467	2	2	0.004	1.00	0.4
I May	447	8	8	0.018	1.00	1.8
II May	460	21	21	0.046	1.00	4.6
III May	347	35	40	0.115	1.14	10.1
IV May	250	46	59	0.236	1.28	18.4
I June	122	35	46	0.377	1.31	28.7
II June	106	26	41	0.387	1.58	24.5
III June	37	20	33	0.892	1.65	54.1
IV June	11	5	11	1.000	2.20	45.5
Total		198	261	0.118	1.32	8.9
Successful nests		51	72	0.103	1.41	7.3

able to control for many of the potential causes of nonrandom distribution patterns of parasitic eggs listed above, even if parasitic females actually laid their eggs randomly.

STUDY AREA AND METHODS

We studied Red-winged Blackbirds in a series of marshes located in the Columbia National Wildlife Refuge in central Washington State. The area and general ecology of blackbirds are described by Orians (1980). Observations were made each year from 1977 through 1983, from mid-March, before nesting began, to mid- to late-June, when at least 95% of annual breeding was completed. Marshes were searched for new nests and nests were checked for progress usually every three days. Because redwing nests are easy to find, all nests on the study area were located. The first cowbird eggs were laid in redwing nests during the last week of April, roughly one month after the first redwing nests were started. Thus, early nesting redwings escaped cowbird parasitism entirely. Because the intensity of parasitism (percent of nests parasitized) and number of nests available to be parasitized changed dramatically during the breeding season, we divided each month into four periods (7, 8, 7[8] and 8 days, respectively), long enough to yield samples large enough for statistical analysis, but short enough that nest availability and number of laying female cowbirds did not change very much.

We performed analyses both using all redwing nests, whether or not they were parasitized, and just the sample of parasitized nests. Analysis of the complete sample can reveal whether cowbirds find it more difficult to locate some nests than others. Analysis of the sample of parasitized nests can reveal whether female cowbirds avoid laying in already parasitized nests. Redwings are not known to eject cowbird eggs or to desert their nests when they are parasitized (Rothstein 1975).

Because weekly sample sizes are often small and because the seasonal pattern of egg laying of Red-winged Blackbirds and Brown-headed Cowbirds were similar among years (Fig. 1), except for 1979, data from different years are pooled by week in our analyses.

TABLE 2

THE OBSERVED AND EXPECTED DISTRIBUTION OF BROWN-HEADED COWBIRD EGGS IN THE NESTS OF RED-WINGED BLACKBIRDS BY WEEKLY PERIODS

Period	Distribution of cowbird eggs (N)						Chi-square[a]	df
	0	1	2	3	4	5		
IV Apr.								
Observed[b]	465	2	—	—	—	—		
$Expected_1$	465	2	—	—	—	—	0.0	1
$Expected_2$		2	—	—	—	—		
I May								
Observed	439	8	—	—	—	—		
$Expected_1$	439	8	—	—	—	—	0.0	1
$Expected_2$		8						
II May								
Observed	439	21	—	—	—	—		
$Expected_1$	439	21	—	—	—	—	0.0	1
$Expected_2$		21	—	—	—	—		
III May								
Observed	312	31	3	1	—	—		
$Expected_1$	309	36	2	—	—	—	2.3	2
$Expected_2$		30	5	—	—	—	0.1	1
IV May								
Observed	204	37	7	1	—	1		
$Expected_1$	197	47	5	1	—	—	3.7	3
$Expected_2$		35	9	2	—	—	0.4	2
I June								
Observed	87	27	6	1	1	—		
$Expected_1$	84	32	6	—	—	—	1.0	2
$Expected_2$		26	9	—	—	—	0.3	1
II June								
Observed	80	16	6	3	1	—		
$Expected_1$	72	28	5	1	—	—	8.5	2
$Expected_2$		15	8	3	—	—	0.5	2
III June								
Observed	17	13	3	2	2	—		
$Expected_1$	15	16	6	2	—	—	4.5	3
$Expected_2$		11	6	3	—	—	2.4	2
IV June								
Observed	6	1	2	2	—	—		
$Expected_1$	4	4	3	—	—	—	3.6	2
$Expected_2$		2	2	2	—	—		

TABLE 2
CONTINUED

Period	Distribution of cowbird eggs (N) 0	1	2	3	4	5	Chi-square[a]	df
Total								
Observed	2039	156	27	10	4	1		
$Expected_1$	1991	235	14	—	—	—	81.4***	2
$Expected_2$		145	42	8	2	—	8.3*	2
Successful nests								
Observed	650	38	9	1	2	1		
$Expected_1$	632	65	3	—	—	—	37.6***	2
$Expected_2$		35	13	4	—	—	1.4	2

[a] Significant differences between observed and expected values are indicated: * $P < 0.05$, *** $P < 0.001$.
[b] $Expected_1$ = expected values when zero class is included. $Expected_2$ = expected values using a truncated Poisson distribution excluding the zero class.

RESULTS

The number of cowbird eggs in weekly samples increased to a maximum the last week of May and thereafter decreased to the last week of June (Table 1). However, because the number of redwing nests started each week decreased steadily during the same period, the proportion of nests parasitized increased throughout the breeding season (Fig. 1).

A random distribution model could be rejected in only one of the weekly samples, during which there were more nests without cowbird eggs than expected by chance (Table 2). This may be an artifact of the differences in parasitism rates in 1979 because if 1979 is excluded from the analysis the random distribution model cannot be rejected ($\chi^2 = 4.7$, $0.05 < p < 0.10$). The truncated Poisson distribution using only parasitized nests could not be rejected in any of the weekly samples (Table 2). However, with the entire sample, a random model could be rejected: (1) if the zero class was included because there were more nests without or with several cowbird eggs and fewer nests with a single cowbird egg than expected (both for the total sample and for successful nests only), and (2) for parasitized nests, because there were more nests with a single cowbird egg or with 3–5 cowbird eggs and fewer nests with two cowbird eggs, than expected (for the total sample for successful nests the random distribution model could not be rejected).

Most of the nest failures were due to predation. However, there was no significant difference between the rate of nest failures (percent of nests lost prior to fledging) in parasitized and unparasitized nests within any weekly period or for the total sample ($\chi^2 = 1.71$, $P > 0.3$, df = 1). The proportion of successful nests was 31.9% for unparasitized nests and 25.8% for parasitized nests, respectively. Thus, predators found unparasitized nests as readily as they found parasitized nests.

DISCUSSION

Our data support the hypothesis that female cowbirds lay their eggs randomly in nests of Red-winged Blackbirds. There is no evidence that they avoided already parasitized nests or that the nests they failed to parasitize were more difficult to find or more heavily defended than the nests in which they did lay eggs. Although predators do not search for redwing nests in the same manner as female cowbirds, the fact that predation rates were not statistically different on parasitized and unparasitized nests suggests that unparasitized nests were not more difficult to find.

However, if we had analyzed our data by pooling them over the entire breeding season, we would have concluded that cowbirds tried to lay in already parasitized nests. The apparent excess of unparasitized nests would have been due to inclusion of nests started before the first cowbirds laid their eggs. The apparent excess of nests with more than one cowbird egg in the pooled sample was due to the fact that the number of suitable host nests relative to the number of laying female cowbirds varied temporally. Actually, however, when the intensity of parasitism was high, there were as many cases of multiple parasitism as expected under the assumption of random laying.

The nine marshes used in our study ranged from an average of 19 to 93 redwing nests per year. Parasitism rates varied strikingly among marshes, but they were not related to number of redwing nests ($N = 9$, $r = 0.06$, $P = 0.44$). Robertson and Norman (1977) found that rates of parasitism by cowbirds on redwings were inversely proportional to redwing nesting density, suggesting that the presence of more adults made it more difficult for cowbirds to gain access to the nests. Our failure to find such an effect may be due to the fact that our study marshes are mostly strip marshes only one territory in depth. Consequently, most territories abut only two others, regardless of marsh size, and it should not be more difficult for cowbirds to approach nests in the large marshes than in the smaller ones.

We do not expect our results necessarily to be characteristic of all interactions between cowbirds and their hosts. For some host species, unlike redwings, incubation periods differ from those of cowbirds. Also the redwing is a relatively large host. Male cowbirds are larger than female redwings, but female redwings are slightly larger than female cowbirds. Therefore, if a female encountering an already parasitized nest is able to remove another host egg and substitute for it her own egg, her offspring has a good chance of experiencing less nestling competition than if she had laid in an unparasitized nest (Roskaft, Orians and Beletsky, unpubl. data). However, if the host is smaller than a cowbird, a nestling cowbird is a stronger competitor than a host nestling. Multiple parasitism of these species should be avoided. This would be especially true if parasitic females maintained exclusive laying territories because, in that case, a parasitic egg in a nest is highly likely to be hers. If there is overlap in laying areas of different parasitic females, so that a female may not know if a parasitic egg she finds in a nest is her own, ejection of a parasitic egg would be risky. A statistical study such as ours could reveal avoidance of already parasitized host nests if that were occurring.

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